ON A COLLECTION OF FRESHWATER GASTROPOD MOLLUSCS FROM THE ETHIOPIAN HIGHLANDS

BY

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Pp. 285–312 ; *Plates* 8–9 ; *Map* ; 33 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 8 No. 6
LONDON : 1962

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series, corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 8, *No.* 6 *of the Zoological series.*

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Issued March, 1962 *Price Twelve Shillings and Sixpence*

ON A COLLECTION OF FRESHWATER GASTROPOD MOLLUSCS FROM THE ETHIOPIAN HIGHLANDS

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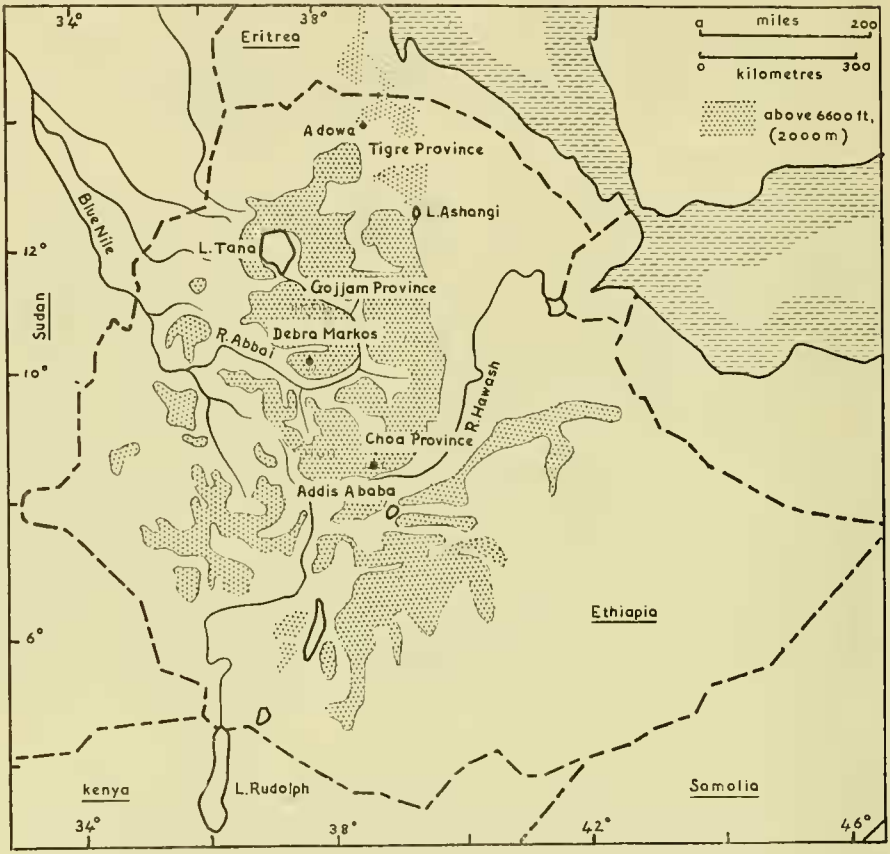
In 1957 the Chokke Mountains which lie to the south of Lake Tana in Gojjam Province, Ethiopia, were visited by a Cambridge botanical expedition, and a zoologist accompanying the expedition, Mr. W. J. Ballantine, undertook to make a collection of land and freshwater molluscs from the area with particular regard to the altitudinal limits of the distribution of *Bulinus forskali*. He brought back an excellent collection of well-preserved specimens, although *B. forskali* was not found, and the freshwater gastropods from that material are the subject of this paper.

The areas covered by the expedition lie to the north-east and south of Debra Markos (37° 43′ E. 10° 20′ N.), the provincial capital, within twenty-five miles of the town which is situated at 8,100 ft. This part of the Ethiopian Highlands is bounded to the east and south by the River Abbai which flows southward out of Lake Tana and further downstream becomes the Blue Nile (Map 1). Collections were made between 7,000 and 12,000 ft. and a list of stations relevant to this part of the collection is given in an appendix to this paper, together with some data on the climate of the area. Locality numbers given in the text refer to this list. The freshwater gastropods collected belong to two families only, the Planorbidae and the Lymnaeidae. The list of synonyms given for each species is primarily a regional one and is not intended to be complete for the whole of Africa.

HISTORICAL

The major work on the Mollusca of Ethiopia is Jickeli's account of the non-marine molluscs of North-east Africa published in 1874. Before this date the eastern part of the highland region had been visited by Blandford (1870) who included descriptions of some molluscs in the general account of his journey. Subsequent authors who have described species or provided records of already known forms from Ethiopia are Bourguignat (1883 and 1885), von Martens (1897), Pollonera (1898), Neuville & Anthony (1906), Piersanti (1940) and Verdcourt (1956 and 1960). There are many accounts of the Mollusca of neighbouring Italian and French Somaliland of which that of Germain (1904) may be specially mentioned. Bacci (1951) has compiled a list of both terrestrial and aquatic species for Abyssinia (Ethiopia and Eritrea) and Italian Somaliland and provides a comprehensive list of references. For this reason only those papers published prior to 1951 which are strictly relevant to the material described are mentioned in the present paper, although an attempt has been made to provide a complete list of work published since that date. A great deal of information concerning the freshwater gastropods of the area is provided by Ayad (1956)

who carried out a survey, under the auspices of the World Health Organization, to determine the incidence and mode of transmission of human schistosomiasis.



Map 1. Ethiopia and surrounding territories (redrawn from Ayad, 1956).

Family Planorbidae

Bulinus sericinus (Jickeli, 1874)

Isidora sericina Jickeli, 1874.
Isidora shackoi Jickeli, 1874.
Isidora sericina var. *harpula* Pollonera, 1898.
Isidora shackoi mut. *minima* Pollonera, 1898.
Bullinus (*Isidora*) *mussolinii* Piersanti, 1940.

Localities (figures in brackets indicate the numbers of individuals in the samples) 1 (296) ; 2 (48) ; 3 (21) ; 4 (6) ; 5 (5). Most of the specimens were collected at the margins of streams on vegetation and mud.

There is a good deal of variation in the shell characters both between different population samples and within the same sample. The shells from locality 1 (Pl. 8) have the whorls not markedly inflated or ribbed and the majority are thickly coated with a black deposit. The degree of exsertion of the spire is variable, the more elongated shells (Pl. 8) resembling *Bulinus shackoi*. The ratio of shell length (*l*) to aperture length (*ml*) is plotted against shell length in Text-fig. 1 ; this illustrates that there is a tendency for the ratio to increase with the size of the shell although at any

TABLE I.—*The Variation in the Ratio Total Length/Aperture Length (l/ml) in Shells of* Bulinus sericinus *from Three Localities*

Locality	Size group* (mm.)	Number of specimens	Mean *l/m*	Range *l/ml*
1	11	2	1·64	1·55–1·74
	10	3	1·49	1·42–1·61
	9	17	1·49	1·37–1·36
	8	26	1·49	1·29–1·78
	7	25	1·46	1·30–1·68
	6	53	1·46	1·30–1·78
	5	66	1·35	1·21–1·61
	4	63	1·32	1·21–1·52
	3	27	1·32	1·21–1·52
	2	1	1·32	—
2	11	1	1·51	—
	10	1	1·49	—
	9	3	1·41	1·30–1·52
	8	8	1·39	1·29–1·48
	7	17	1·35	1·21–1·44
	6	12	1·34	1·27–1·45
	5	1	1·33	—
	4	3	1·23	1·19–1·27
	3	1	1·30	—
3	8	4	1·28	1·22–1·32
	7	2	1·29	1·29–1·30
	6	6	1·36	1·30–1·44
	5	4	1·28	1·21–1·35
	4	4	1·22	1·18–1·25

* Shells grouped according to total length, i.e., 10 mm. group contains individuals of 10·0–10.9 mm. length.

particular size there is a wide variation in the actual values. The aperture is ovate and the columellar margin is widely reflexed, almost closing the umbilicus. From locality 2 the majority of the specimens are empty shells of a reddish-brown colour and more globular in appearance (Pl. 8) than those from locality. 1 The whorls are inflated and, in some of the smaller specimens, there is a marked " shoulder " on the upper part of the whorls. The values of the ratio *l/ml* are included in Text-fig. 1, and are generally smaller than those obtained from locality 1, although there is

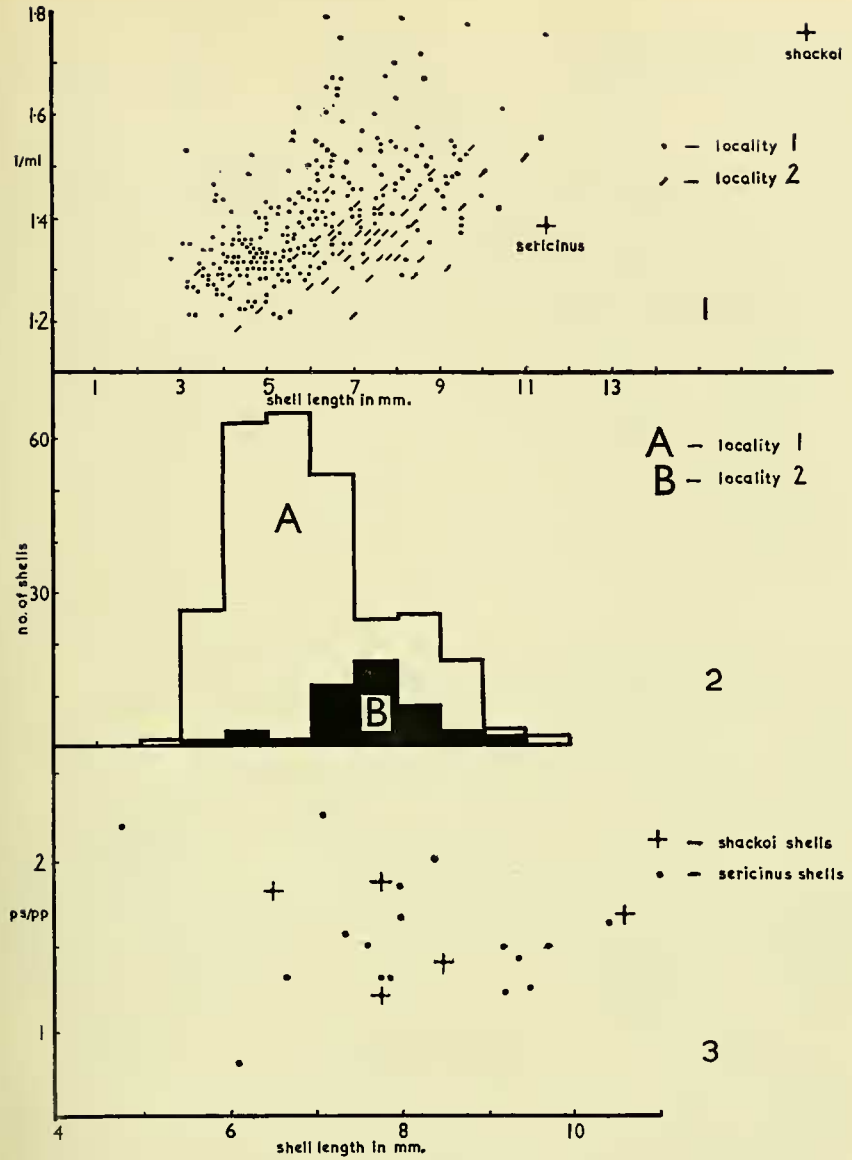
extensive overlapping between the two populations. Many of the shells have fine, regularly spaced ribs whose size is increased by frayed folds of periostracum. In some specimens these ribs are confined to the upper whorls but in others up to 8 mm. shell length they are present over the whole shell. The shells from locality 3 show a degree of inflation that is intermediate between the preceding populations, and ribs are present on the upper whorls of most of them (Pl. 8). In order to show the change of form with size, the variation at a particular size, and the variation between different populations, the mean values of *l*/*ml* have been calculated for shells from localities 1–3 which have been divided into millimetre size groups (Table I). In the sample from locality 4 there is a single specimen with inflated whorls and a rounded aperture while the remaining shells resemble the more slender specimens from locality 1 and lack ribs. The five specimens from locality 5 have reddish-brown shells with inflated whorls and widely reflexed columellar margins and no ribs. Besides the differences in the form of the shells there appear to be differences in the size composition of the two largest collections (localities 1 and 2, Text-fig. 2).

There is great variation in the intensity of pigmentation of the external surface of the mantle. The least and most heavily pigmented mantles from localities 1 and 2 are illustrated in Text-figs. 8 and 9. The epithelium overlying the visceral hump is evenly and relatively deeply pigmented. There is no trace of a ridge on the kidney, but between the kidney and the rectum is an intermediate mantle ridge running across the roof of the pallial cavity parallel to the rectum, extending from a point approximately level with the proximal end of the kidney as far as the mantle collar (Text-fig. 10).

In the male copulatory organ the relative proportions of the penis sheath and the preputium vary widely, particularly in the smaller specimens, but, with one exception, the sheath was found to be longer than the preputium. The ratio of the length of the penis sheath to that of the preputium (*ps*/*pp*) is plotted against shell length for some specimens from locality 1 (Text-fig. 3). In those from locality 2 the ratios lie between 1·0 and 1·88 ; a single aphallic specimen was found in this sample. The upper part of the penis sheath is swollen and is usually wider than the broadest part of the preputium (Text-figs. 6 and 7). A short epiphallus is followed by the thick-walled eversible part of the penis which occupies almost the whole of the upper part of the lumen of the sheath. Four stages in the development of the accessory genital glands and the distal genitalia are shown in Text-figs. 4–7, from which it can be seen that the male copulatory organ is relatively larger in the smaller specimens. Both the male and female genitalia increase rapidly in size between a shell length of 7 and 8 mm. and full hermaphrodite maturity is probably reached at a length of about 8 mm. In mature specimens the spermatheca is subspherical in shape and the spermathecal duct is about equal to its longest axis.

The seminal vesicle is formed by a thickened coiled part of the hermaphrodite duct that bears numerous papillae. In the ovotestis of a specimen of 7 mm. there are about 40 acini arranged regularly in three rows.

There are 23–25 teeth in each half-row of the radula. The shape of the mesocone of the lateral teeth (Text-fig. 11) is neither sharply conical as illustrated by Mandahl-Barth (1957*b*) or bluntly arrow-headed (Mandahl-Barth, 1960). Transition from

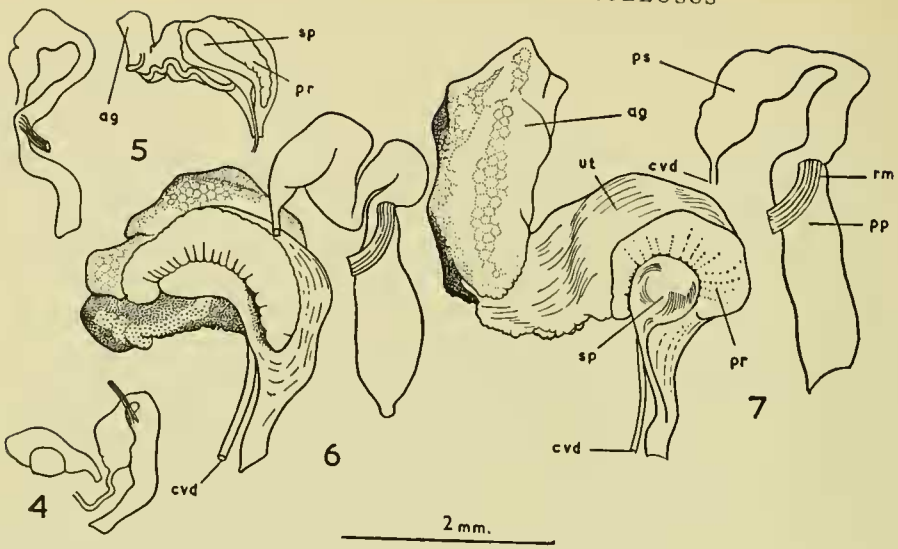


Bulinus sericinus (Jickeli)

FIG. 1. The ratio of shell length/aperture length (*l/ml*) plotted against shell length for shells from localities 1 and 2.

FIG. 2. Size frequency histogram for the samples from localities 1 and 2.

FIG. 3. The ratio of length of penis sheath to length of preputium *ps/pp*) plotted against shell length for specimens from locality 1.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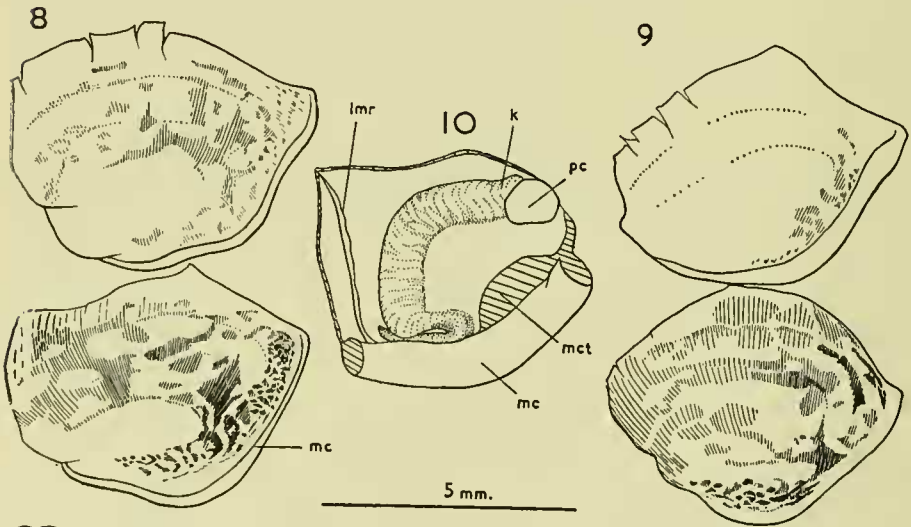
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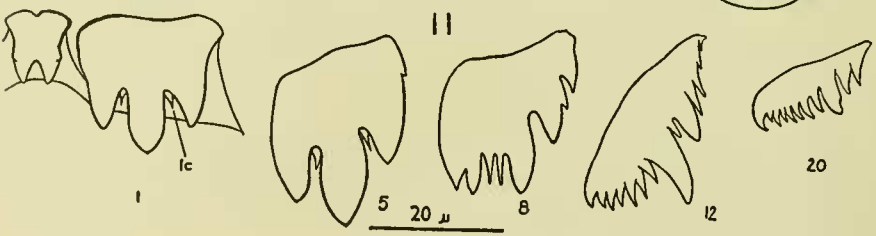
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lateral to marginal teeth takes place between longitudinal rows 6 and 8. Two small interstitial cusps which do not appear to have been described previously in any bulinid snail are present on either side of the mesocone in the majority of lateral teeth.

In his description of *Isidora sericina* Jickeli gives the type locality as the River Toquor at Mekerka in Hamasen Province. The precise position of this locality is uncertain but it probably lies near Asmara in what is now Eritrea. Jickeli described four specimens with markedly exserted spires from the same place as a separate species, *Isidora shackoi*. He could find no difference between the radulae of the two forms and considered the possibility that they might in fact be no more than variants of the same species but rejected this idea because of the marked differences between the shells. The ratios of *l/ml* plotted in Text-fig. 1 provide an index of the degree of exsertion of the spire and included in this figure are the ratios calculated from Jickeli's measurements of *sericinus* and *shackoi*. Although the largest specimen from the Debra Markos area is only 11·5 mm. in length, while the type of *shackoi* is 17 mm. long, the value of *l/ml* for *shackoi* (1·75) lies within the range of variation present in the Debra Markos material, which includes a complete gradation of form between *shackoi* and typical *sericinus*. Dissections have been made of specimens with shells of *shackoi* proportions (for this purpose regarded as having the ratio *l/ml* greater than 1·6) and no anatomical differences have been found between them and typical *sericinus* (Text-fig. 3). It appears that the two species were originally described from extreme variants from a single population.

The strongly ribbed forms found in some of the samples from the Debra Markos area correspond to *Isidora sericina* var. *harpula* of Pollonera from Asmara and Debaroa. Pollonera also described some specimens of 7 mm. shell length as a mutant *minima* of *I. shackoi*; many smaller specimens having shells of *shackoi* proportions occur in the present material. Piersanti (1940) illustrated a very inflated form with a shouldered body whorl and depressed spire as *Bullinus sericinus* (Jickeli) and figured and described another form which appears to be identical with typical *sericinus* as *Bullinus* (*Isidora*) *mussolinii*. Re-examination of the material described by Wright (1956) as *B. sericinus* from Senegal indicates that it should not have been referred to this species but to *B. truncatus rohlfsi* (Clessin).

The relationships of *B. sericinus* are not easy to determine. Haas (1935) suggested that it is a form of *B. truncatus* while Mandahl-Barth (1957*b*) placed it in the *tropicus*

Bulinus sericinus (Jickeli)

FIGS. 4–7. Stages in the development of the accessory genital glands and male copulatory organ—

4. at 6·1 mm. shell length; 5. at 7·1 mm. shell length; 6. at 8 mm. shell length; 7. at 9·2 mm. shell length.

FIGS. 8 and 9. Examples of mantles showing the variation in the degree of pigmentation of the outer surface—

8. Lightly and deeply pigmented specimens from locality 1. 9. Lightly and deeply pigmented specimens from locality 2.

FIG. 10. Inner surface of mantle.

FIG. 11. Radula teeth.

group but mentioned that intermediates between *sericinus* and both *truncatus* and *tropicus* had been seen. The differences between the *truncatus* and *tropicus* groups are not well defined and it is possible that they are not really distinct. According to Mandahl-Barth the members of the *tropicus* group have triangular mesocones on their lateral radula teeth, they are rarely aphallic, and none of the species are known to act as intermediate hosts of *Schistosoma haematobium* ; the species of the *truncatus* group have arrow-headed shaped mesocones, are frequently aphallic and *B. truncatus* is the principal snail host for urinary schistosomiasis in North Africa and the Middle East. The mesocones of the lateral teeth in the Debra Markos material are more arrow-headed than triangular and a single aphallic specimen was found in one of the samples. These characteristics indicate a closer affinity with the *truncatus* rather than the *tropicus* group. This is the conclusion reached by Mandahl-Barth (1960) after examination of material from Lake Tana, and he has reduced *sericinus* to a subspecies of *B. truncatus*. In the present paper the specific status of *sericinus* has been preserved for reasons which are given in the general discussion. It has not been proved that *B. sericinus* can act as a host of *Schistosoma*, but this seems likely to be the case as there are extensive highland areas in Ethiopia from which *S. haematobium* has been reported and in which no other species of *Bulinus* has been found (Ayad, 1956).

Until living material of *B. sericinus* becomes available for further study it is perhaps best to retain this name for the *Bulinus* from the highland regions of Ethiopia although subsequent work may well prove that it is not a distinct species.

Biomphalaria rueppelli (Dunker)

Planorbis rüppellii Dunker, 1848.
Planorbis adowensis Bourguignat, 1879.
Planorbis herbini Bourguignat, 1883.
Planorbis cecchii Pollonera, 1887.
Planorbula boccardi Pollonera, 1898.
Planorbis bozasi Rochebrune & Germain, 1904.

Localities : 2 (69) ; 3 (61). The specimens were collected from broad-leaved vegetation in the shallows (2) and from floating weeds and rocks in a small pool overhung by undergrowth (3).

There is no difference in the appearance of the shells from the two localities. The largest specimens have a diameter of 10–11 mm. and consist of 4–4½ whorls which are rounded on the upper surface except for the last one which is flattened toward the aperture (Pl. 9). In the majority the first two whorls are more deeply sunk on the upper side, and there is a blunt angulation on the under surface of all the whorls near the suture. There is no sculpture apart from fine irregular growth lines. The mean ratios of maximum diameter to height (*d*/*h*), maximum diameter to diameter of umbilicus (*d*/*ud*), and diameter of umbilicus to height (*ud*/*h*) are given for the individuals of both populations grouped according to their diameter into size groups of 1 mm. (Table II). As the last whorl was deflected to a variable extent towards the aperture the height of the last whorl only, and not the total height of the shell, was measured. The ratios *d*/*h* and *d*/*ud* for specimens from locality 3 are plotted against

TABLE II.—*The Variation in the Proportions of the Shells of* Biomphalaria rueppelli *from Two Localities*

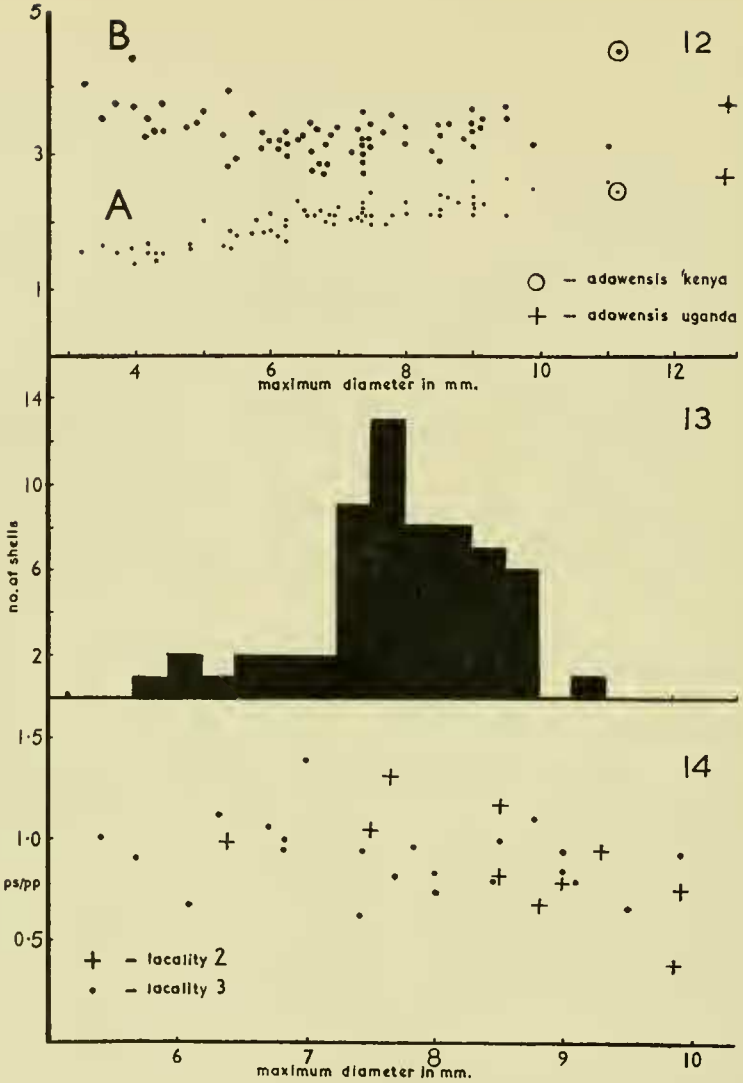
Locality	Size group* (mm.)	Number of specimens	Mean *d/h*	Mean *d/ud*	Mean *ud/h*
2	10	1	2·64	3·00	0·88
	9	13	2·64	3·08	0·72
	8	16	2·14	3·04	0·71
	7	22	2·15	3·13	0·69
	6	4	2·00	3·13	0·64
	5	3	1·89	3·23	0·58
	4	3	1·60	2·67	0·60
3	11	1	2·56	3·08	0·84
	10	—	—	—	—
	9	9	2·33	3·40	0·69
	8	8	2·22	3·23	0·69
	7	14	2·12	3·22	0·67
	6	17	1·99	3·10	0·64
	5	8	1·83	3·30	0·56
	4	8	1·51	3·44	0·44
	3	4	1·54	3·89	0·40

* Shells grouped according to maximum diameter, e.g., 10 mm. group contains individuals of 10·0–10·9 mm. diameter.

diameter in Text-fig. 12 and it is evident that all vary according to the size of the shell ; *d/ud* is largest in the smallest specimens and decreases to remain at a relatively constant level in the larger specimens ; *d/h* increases steadily over the whole of the size range present in the sample.

A light grey pigmentation on the outer surface of the mantle is concentrated at the borders of the kidney. The disposition of ridges within the pallial cavity and the structure of the pseudobranch and the pulmonary siphon closely resemble that described in *Biomphalaria pfeifferi* by Schutte & van Eeden (1957*b*) and their terminology will be followed. Between the kidney (on which there is no ridge) and the rectum is an intermediate mantle ridge (IMR) which extends from the ventral surface of the mantle collar to the level of the pericardium (Text-fig. 19). On the left side of the rectum is a very large lateral rectal ridge (LRR) which is highly convoluted with a thickened free edge. A median rectal ridge (MRR) runs from the edge of the pulmonary opening along the right side of the rectum for a short distance. A continuation of the lateral rectal ridge runs along the entire length of the anal lobe.

There is considerable variation in the ratio of the length of the penis sheath (*ps*) to that of the preputium (*pp*), the extremes of *ps/pp* being 1·5 in a shell of diameter 7 mm. and 0·5 in one of 9·5 mm. (Text-fig. 14). The tip of the penis lies either immediately proximal or immediately distal to the junction between the sheath and the preputium. The preputium is the most deeply pigmented part of the copulatory organ and longitudinal concentrations of pigment can usually be detected which overlie the muscle pillars on the inner wall. These muscle pillars are opposed to each



Biomphalaria rueppelli (Dunker)

FIG. 12. The ratio of (A) maximum diameter of shell to shell height (*d/h*), and (B) maximum diameter to umbilicus diameter (*d/ud*) plotted against maximum diameter for shells from locality 3.

FIG. 13. Size frequency histogram for the sample from locality 2.

FIG. 14. The ratio of length of penis sheath to length of preputium (*ps/pp*) plotted against maximum diameter of shells from localities 2 and 3.

other, that on the right side of the preputium being larger than that on the left and in some specimens the left pillar may be absent (Text-fig. 20). Two muscles are inserted at the junction between the penis sheath and the preputium (Text-fig. 17), the larger (*rm* 2) passes ventrally and is attached to the columellar muscle, and the smaller (*rm* 1) originates on the dorsal wall of the head region. In addition fine fibres are inserted in rows on each side of the preputium (*rm* 3 and 4) and are also attached beneath the dorsal wall of the head. The structure of the prostate is difficult to make out because of the retracted condition of the specimens, it closely resembles that of *B. pfeifferi* as described by Schutte & van Eeden (l.c.) although there appear to be at least 12 rather than 9–12 primary diverticula. The majority of the diverticula are branched and some bear tertiary diverticula.

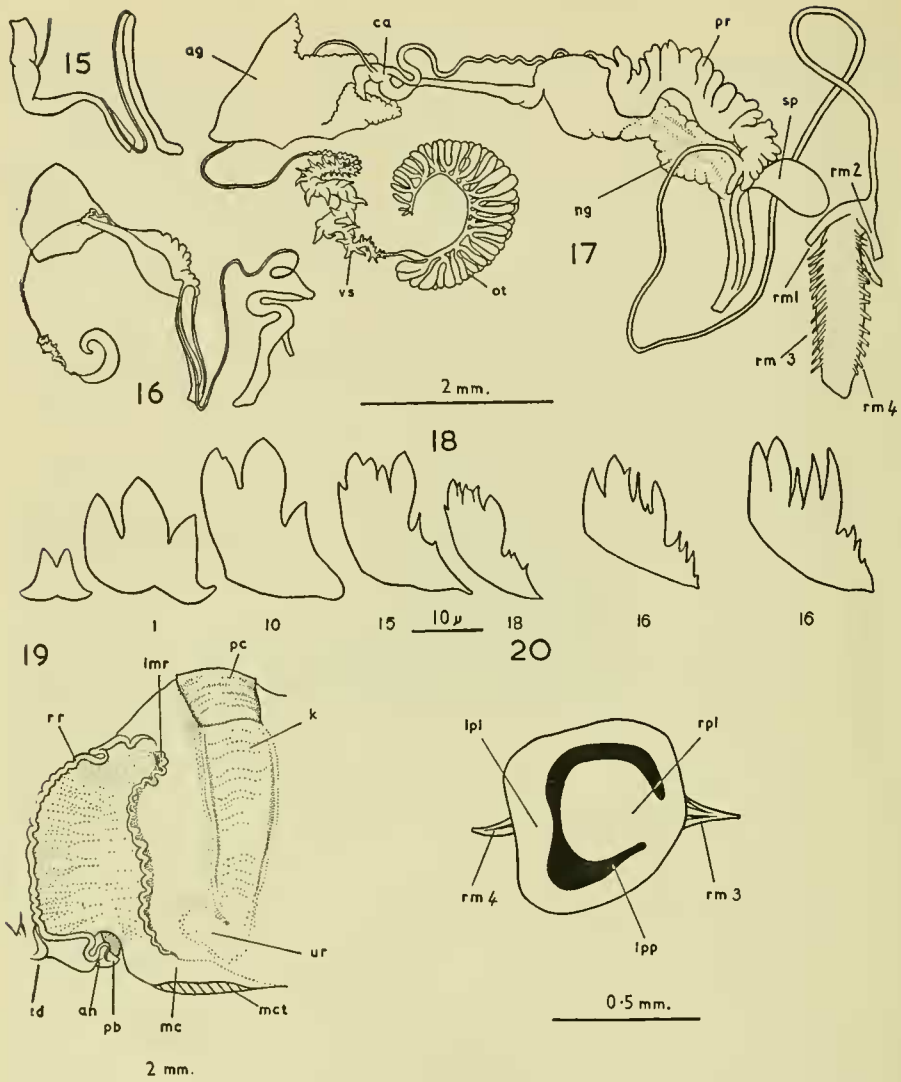
The female system of *B. rueppelli* resembles that described for other *Biomphalaria* and appears to be of little taxonomic importance. In mature specimens the spermatheca is flattened against the other organs and its periphery is more or less circular. The spermathecal duct is relatively long and opens into the vagina near the female genital pore (Text-fig. 17).

The ovotestis consists of a variable number of pairs of branched acini ; the hermaphrodite duct is dilated close to the bases of the first pair of diverticula (Text-fig. 17). The dilatation of the hermaphrodite duct that forms the vesicula seminalis begins close to the ovotestis and the thickness of the coiled duct increases rapidly and decreases again distally. This part of the duct bears finger-like processes which are replaced anteriorly by more translucent rounded vesicles.

Three stages in the development of the accessory genital glands and the male copulatory organ are shown in Text-figs. 15–17. These organs increase in size rapidly between a shell diameter of 6 and 8 mm. and though protandry is not so marked as in *Bulinus sericinus* the male system appears to be better developed at a smaller size. Full sexual maturity is probably reached between a shell diameter of 7 and 8 mm.; there is no apparent change in shell form correlated with this.

In most of the radulae examined there are 22 teeth present in each half-row. The ectocones of the laterals are triangular and the endo- and mesocones are more or less lanceolate ; no interstitial cusps were observed (Text-fig. 18). In a few specimens bifurcation of the endocone occurs in the 10th longitudinal row of teeth, and in general the transition between the lateral and marginal teeth takes place between the 12th and 15th rows. There is great variation in the form of the lateral teeth and the ectocone is not always divided into four cusps as described by Mandahl-Barth (1957*a*) ; although in no case was it undivided as is the typical condition in S. African *B. pfeifferi*. In one radula the whole longitudinal row of 5th lateral teeth is bicuspid resembling the centrals.

Bourguignat (1879) described *Planorbis adowensis* from a shell of *Planorbis rueppelli* Dunker, with rapidly increasing whorls and a relatively small umbilicus, illustrated by Jickeli (1874). The internal anatomy of *rueppelli* and *adowensis* was first described by Ranson & Cherbonnier (1952) from material collected at great distances from the type localities. Mandahl-Barth (1957*a*) observed that populations usually consist of either typical *rueppelli* or *adowensis*, but concluded from the occurrence of mixed populations with some specimens intermediate between the two that *adowensis* should



Biomphalaria rueppelli (Dunker)

FIGS. 15–17. Stages in the development of the accessory genital glands and the male copulatory organ—

15. at 5·8 mm. shell diameter ; 16. at 6·5 mm. shell diameter ; 17. at 7·7 mm. shell diameter.

FIG. 18. Radula teeth.

FIG. 19. Pneumostome cut through on right side and mantle turned to the left to show pseudobranch, kidney and pallial ridges.

FIG. 20. Transverse section through preputium.

be regarded as a form of *rueppelli* having no ecological significance. Mandahl-Barth gives measurements of the shells of the *adowensis* form from Uganda and Kenya and these are included in Text-figs. 12 and 14. The Uganda specimens are considerably larger than the Ethiopian shells from the known pattern of variation. However, the *d/ud* ratio for the Kenya sample does appear to lie outside the Ethiopian range of variation ; although *d/ud* increases slowly with size it is unlikely that any individuals of the Ethiopian populations reach the proportions of the Kenya *adowensis*. The anatomy of the Ethiopian specimens also corresponds more closely to *rueppelli* ; the ratio *ps/pp* lies between 0·75 and 1·25 for the majority of the specimens dissected, but it is of interest that in several specimens the sheath is only about half as long as the preputium, a feature which is described as diagnostic of *adowensis* by Mandahl-Barth. A shell from the Debra Markos collection that resembles *adowensis* in the relatively small size of the umbilicus is shown in Pl. 9. It seems likely that future collecting will reveal a complete intergradation between *adowensis* and typical *rueppelli*.

There are several differences between the morphology of the Ethiopian *rueppelli* and that illustrated by Ranson & Cherbonnier (l.c.). These authors depict one retractor muscle at the junction of the penis sheath and preputium instead of two ; the seminal vesicle is different in their material and a posterior thickly coiled part is omitted ; the spermathecal duct is far thicker than in the Ethiopian material ; the diverticula of the ovotestis do not resemble those of the Ethiopian specimens and are depicted as arranged in a single row. In addition the radula teeth illustrated appear to be very worn and thus of little value for comparative purposes.

Schutte & van Eeden (1959*a* and *b*) and Azevedo *et al.* (1957) have made anatomical studies of *Biomphalaria pfeifferi* based on material from South Africa and Mozambique respectively. A comparison of the measurements made on Ethiopian *rueppelli* with those made by Schutte & van Eeden reveals a difference from *pfeifferi* in the relative proportions of the penis sheath and preputium. In *pfeifferi* the preputium is between 0·71 and 1·60 times the length of the sheath and in *rueppelli* between 1·25 and 2·0 times the length of the sheath. Mandahl-Barth (1957*a*) considered *rueppelli* to be a subspecies of *pfeifferi* but more recently (1960) has suggested that the differences between the subspecies of *pfeifferi* are not sufficiently constant to justify their retention and he therefore regards *rueppelli* as a synonym of *pfeifferi*. The observations reported above suggest that it is perhaps premature to treat *rueppelli* as identical with *pfeifferi* and it is therefore regarded here as a separate species.

Gyraulus costulatus (Krauss)

Planorbis costulatus Krauss, 1848.
Planorbis costulatus Jickeli, 1874.
Planorbis stelzneri Dohrn, E. v. Martens, 1869.
Planorbis aethiopicus Bourguignat, 1883.
Caillaudia angulata Bourguignat, 1883.

LOCALITIES : 3 (3).

The specimens were collected with large numbers of *Anisus natalensis* (Krauss) from which they can be readily distinguished by the presence of a carination on the

periphery of the shell and more rapidly widening whorls (Pl. 9). The underside of the shell is concave with the lower surface of the whorls more rounded than the upper. Coarse, regularly spaced ribs are present, and in one specimen areas of both coarse costulation and fine irregular striation are present. This variation of the ornamentation present on a single shell raises doubts about the validity of using sculptural characters for the differentiation of subspecies of *Gyraulus costulatus* as Mandahl-Barth (1954) has done.

Only one shell contained an animal and the condition of this did not allow a detailed anatomical examination. The structure of the penis is like that of other gyraulid snails which have been described ; at the tip there is a grooved stylet with a bulbous base proximal to which lies the opening of the vas deferencs.

Planorbis aethiopicus was described by Bourguignat from one of Jickeli's drawings of *P. costulatus* and is only tentatively included in the list of synonyms given above. It must be mentioned that Ranson (1955) regards it as a distinct species.

Anisus natalensis (Krauss)

Planorbis natalensis Krauss, 1848.
Planorbis abyssinicus Jickeli, 1874.
Planorbis abyssinicus var. *gravieri* Germain, 1904.

Localities : 3 (45) ; 4 (43) ; 5 (30).

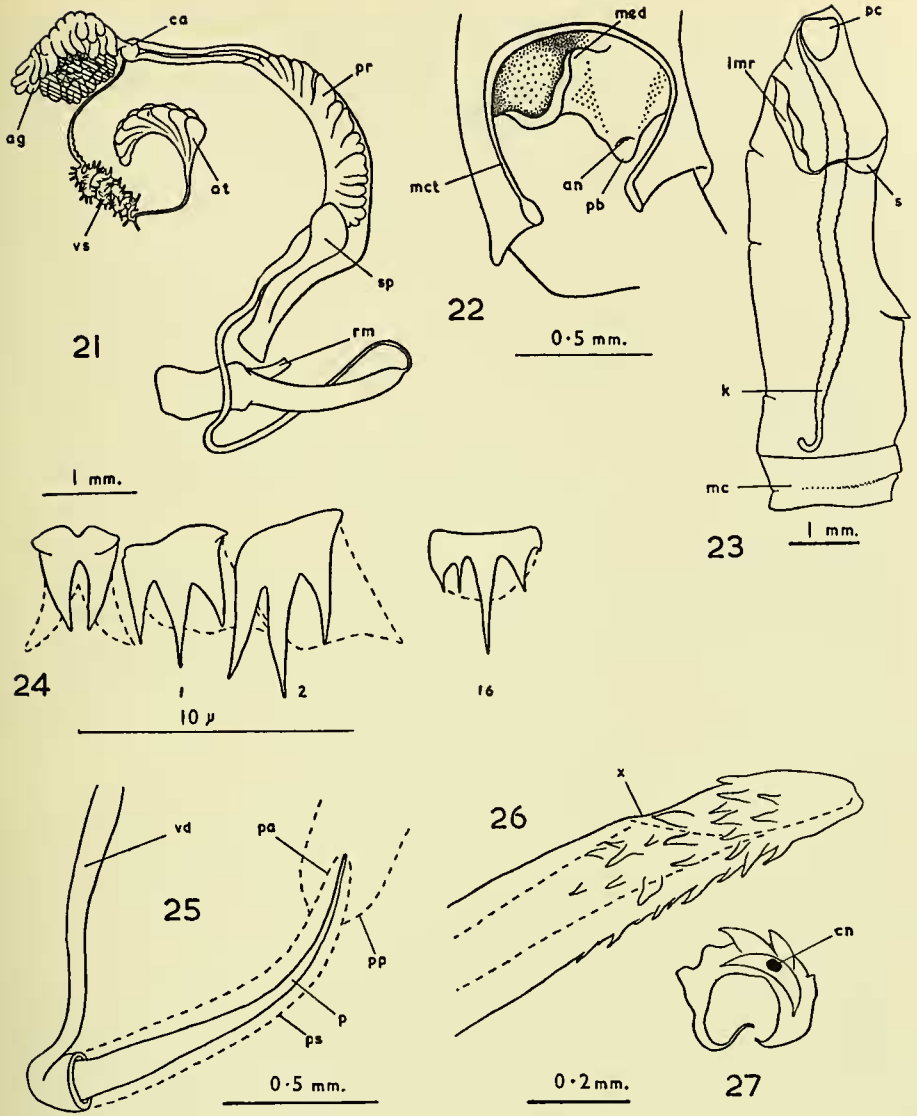
The specimens were collected from small shallow pools overhung by vegetation.

The whorls of the reddish-brown shell increase slowly in width and are separated by a deep suture ; they are slightly flattened on the upperside but are otherwise rounded with a slight angulation towards the underside in some specimens (Pl. 9). No trace of a carination is present. The degree of concavity of the upper surface of the shell is variable but is usually considerably less deep than on the underside. The coiling of many of the shells is loose and irregular, and as a result of the friability of the shells the whorls easily become detached from each other. The aperture is large, and slightly deflected ventrally. Transverse sculpture consisting of numerous, irregular, fine striations is present, and a fine spiral sculpture is usually visible on the under surface. The mean measurements from 10 of the largest shells are as follows :

Diameter : 4·7 mm. Diameter of umbilicus : 2·0 mm. Height : 1·4 mm. Ratio of diameter/diameter of umbilicus : 1·97.

The measurements of the largest specimen are : *d* 5·5 mm.; *ud* 2·3 mm. ; *h* 1·5 mm.; *d*/*ud* 2·39 mm.

The mantle wall is translucent with hardly any pigmentation. The pseudobranch is rudimentary (Text-fig. 22). There is no ridge on the long and narrow kidney (Text-fig. 23) but a conspicuous ridge (IMR) is present on the left-hand side of the roof of the pallial cavity extending from the cardiac end of the kidney to about one-third of its length, and continuous distally with an incomplete septum lying across the mantle cavity. This ridge appears to correspond to the intermediate mantle ridge of *Biomphalaria pfeifferi*.



Anisus natalensis (Krauss)

FIG. 21. Genital system.
FIG. 22. Mantle cut away to show pneumostome and pseudobranch.
FIG. 23. Inner surface of mantle.
FIG. 24. Radula teeth.
FIG. 25. Distal part of vas deferens and penis (penis sheath and preputium shown in broken outline).
FIG. 26. Tip of penis (course of vas deferens in broken outline).
FIG. 27. Transverse section of penis tip at position *x* in Fig. 26.

The size of the male copulatory organ is large in relation to the other reproductive organs (Text-fig. 21), for example, in a shell of diameter 3·5 mm. the length of the preputium is 0·7 mm. and of the penis sheath 0·9 mm. The tip of the penis projects into the preputium and is surrounded by a continuation of the wall of the penis sheath (this has been described by Baker (1945) from European species of *Anisus* and called a papilla). A single retractor muscle is inserted at the junction between the penis sheath and the preputium and has a ventral origin on the columellar muscle. The structure of the penis (Text-figs. 25 and 26) differs from that described in other planorbid genera ; it was examined both in serial sections cut at 6 μ, and by direct dissection. There is no separate stylet but from approximately the mid-point in its length the colour of the penis changes through pale yellow to light brown and the organ becomes increasingly stiff towards the tip. Transverse sections show that this is due to a substance resembling sclerotized arthropod cuticle which is formed at the periphery of the wall as well as internally lining the vas deferens which extends right to the tip of the penis. The size and number of cells in the penis wall decrease progressively towards the tip so that near the opening of the vas deferens there are only a few cells embedded in a solid matrix (Text-fig. 27). The opening of the vas deferens is situated slightly to one side of the penis tip from which project numerous backwardly pointing spines.

The prostate consists of 14–17 lobes (Text-fig. 21), some of which may be sub-divided ; they open into a prostatic duct, the lumen of which is separate from that of the vas deferens, although the two ducts are fused together by their walls and are closely wrapped around the uterus and nidamental gland. The lumen of the prostatic duct opens into the vas deferens a short distance below the base of the most distal lobe of the prostate. In smaller specimens the acini of the ovotestis are arranged in two alternating rows as depicted by Baker for other species of *Anisus* and *Gyraulus*, but in larger specimens this arrangement is disturbed by the proliferation of acini at the base of the gland. The seminal vesicles consist of a thick part of the hermaphrodite duct from which project large numbers of small papillae.

The radula consists of 17 marginal and lateral teeth (Text-fig. 24) in each half-row ; the cusps are long and sharp and resemble those of *Anisus* and *Gyraulus* species depicted by Baker. Transition from marginal to lateral teeth takes place in the 13th and 14th longitudinal rows with the appearance of a cusp between the endocone and the mesocone and another on the outer side of the ectocone.

Apart from the few specimens that conform to *Gyraulus costulatus* (Krauss) all the small planorbid shells collected in the vicinity of Debra Markos resemble *Anisus abyssinicus* (Jickeli, 1874). Jickeli provided no information about the internal anatomy of his species and neither have subsequent authors who have recorded it from widely separated localities in Eritrea, Ethiopia and Somaliland (Germain, 1904 ; Piersanti, 1941 ; Bacci, 1951). By the narrowness of their whorls the Debra Markos specimens resemble *Anisus* more closely than *Gyraulus*, although Baker (1945) includes *abyssinicus* with *natalensis* Krauss, a widespread species in S. Africa, in *Gyraulus*. Connolly (1939) was of the opinion that all the forms of small planorbid mollusc with the shell form of *Anisus* should be regarded as a single species *natalensis* Krauss but makes no reference to *abyssinicus* Jickeli. However, there is a close

resemblance between the present material, that described by Jickeli, and recently collected *Anisus natalensis* from Transvaal.

There are, to our knowledge, no published descriptions of the anatomy of the male copulatory organ of African *Anisus*. Mandahl-Barth (1954), in a description of *A. natalensis* from East Africa, merely states that the internal anatomy of *Anisus* in general resembles that of *Gyraulus*. The penis of the Debra Markos specimens differs markedly from that of *Gyraulus gibbonsi* (Nelson) as described by Binder (1958) and that of *Gyraulus costulatus* from Khartoum and Angola. The latter species possesses a grooved stylet with a bulbous base that is abruptly delimited from the soft part of the penis, and a vas deferens that opens proximally to the stylet. Such a structure is typical of the non-African species for which descriptions are available (Baker, 1945 ; Hubendick, 1955, 1957, 1958). Through the kindness of Dr. J. A. van Eeden specimens of *Anisus natalensis* were obtained from the Transvaal and the structure of the penis was found to be similar, if not identical, to that of the Ethiopian specimens. On the basis of the similarity in both shell and anatomy the material is assigned to *Anisus natalensis* (Krauss) of which *A. abyssinicus* (Jickeli) is provisionally regarded as a synonym. There are some small differences between the shells of the Ethiopian and South African specimens, the importance of which can only be assessed when further samples are available.

The whole question of the relationships between the planorbid genera *Gyraulus*, *Anisus*, and *Armiger* is a long way from clarification. At the present time the anatomical characteristics of *Anisus natalensis* are unique and show that the morphology of the male copulatory organ is far more heterogeneous than when Hubendick (1957) suggested the retention of only a single genus *Anisus*.

Family Lymnaeidae

Lymnaea truncatula (Müller)

? *L. mweruensis* Connolly, 1929.
? *L. peregra* (Müller), Jickeli, 1874.

Localities : 1 (1) ; 2 (3) ; 3 (1) ; 4 (4) ; 6 (86) ; 7 (17) ; 8 (6) ; 9 (62) ; 10 (12) ; 11 (2).

The shells (Pl. 8) closely resemble European specimens and are ornamented to a varying extent with a microsculpture consisting of spiral tracts of fine vertical lines. Measurements of some of the largest shells are given in Table III.

The genital anatomy (Text-fig. 28) is similar to that of European material (Hubendick, 1951) ; the length of the penis sheath is between half and one-third that of the preputium, the prostate bears a single internal fold, and the spermathecal duct is very long and thin.

The central teeth of the radula are asymmetrically bicuspid and on either side of them lie 21–25 lateral and marginal teeth (Text-fig. 29). Hubendick's illustration shows the 1st and 2nd lateral teeth as being tri- and bicuspid respectively, but in the Ethiopian material the 3rd–5th teeth were sometimes bicuspid while the 2nd laterals were not always so.

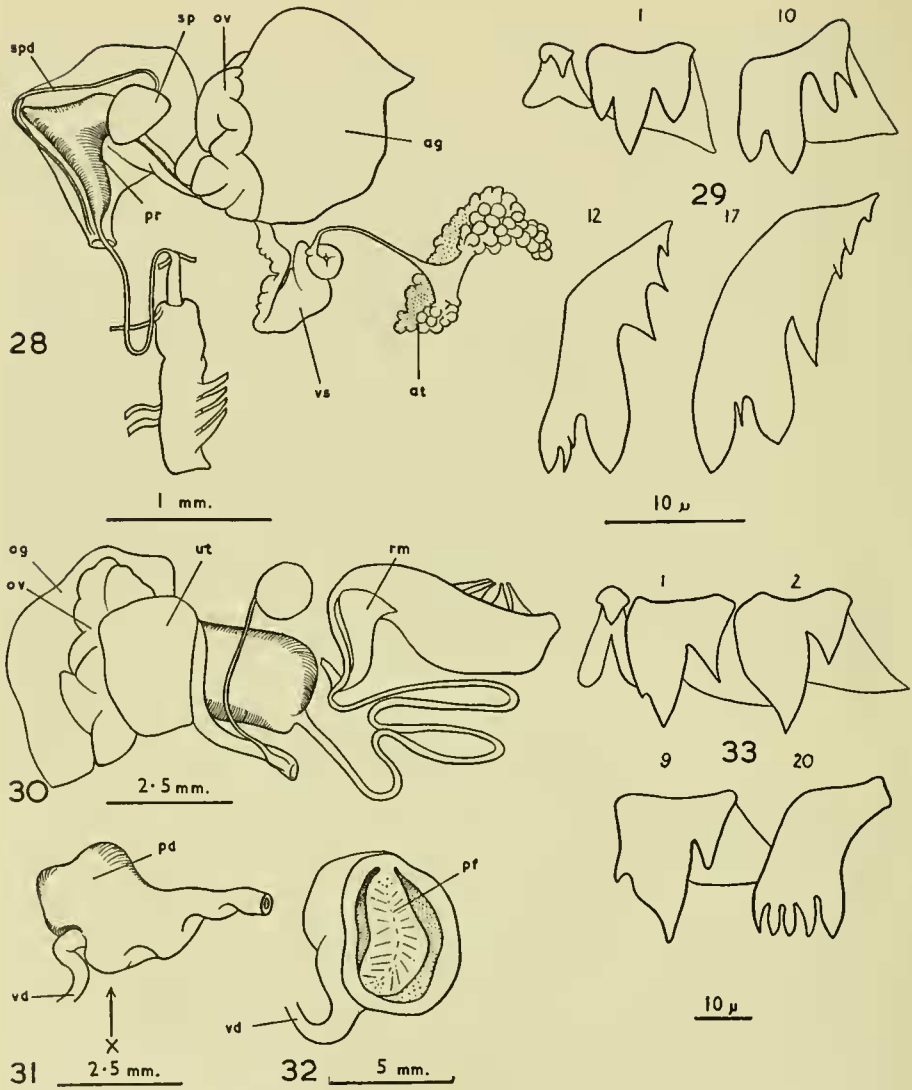


FIG. 28. *Lymnaea truncatula* (Müller), genital system.
FIG. 29. *L. truncatula*, radula teeth.
FIG. 30. *Lymnaea natalensis* (Krauss), genital system.
FIG. 31. *L. natalensis*, lateral view of prostate.
FIG. 32. *L. natalensis*, transverse section through prostate at position *x* in Fig. 31.
FIG. 33. *L. natalensis*, radula teeth.

Transition between the lateral and marginal teeth usually begins in the 9th longitudinal row with the development of one or two small cusps on the outer edge of the ectocone. Teeth in the 12th row which Hubendick shows as being of tricuspid lateral structure, are of multicuspid marginal form. Hubendick omits the basal part of the 17th tooth which in these specimens bears two or three small cusps on the outer side.

Lymnaea truncatula has been recorded from Ethiopia (Jickeli, 1874) and South Africa (Connolly, 1939) and examination of the present material indicates that it is correct to refer Ethiopian material to this widely distributed European species.

Hubendick (1951) examined material from the eastern side of Mount Elgon, Kenya, at 7,000 ft. and concluded that *L. mweruensis* described by Connolly (1929) from the northern side of Mt. Kenya should be regarded as a synonym of *truncatula*. Mandahl-Barth (1954) found a single specimen in the Eldama River at 8,000 ft. and tentatively

TABLE III.—*Shell Proportions of Large Specimens of* Lymnaea truncatula *from Ethiopia: (Shell Length/Aperture Length and Shell Length/Aperture Width)*

Shell length (mm.)	*l/ml*	*l/mw*
8·7	1·45	2·72
7·7	1·64	2·48
6·5	1·76	2·83
6·3	2·03	2·03
6·3	1·75	2·86
6·2	1·77	2·58
5·9	1·84	2·68
5·7	1·84	3·00
5·6	1·75	2·54
5·5	1·96	2·75
5·2	1·79	2·88
4·9	1·81	2·88
4·4	1·76	2·75
Type specimen of *L. mweruensis* Connolly		
6·1	1·85	3·05

recorded it as *L. mweruensis*. The type specimen of *mweruensis* (Pl. 8) has been compared with the Debra Markos material from which it can be readily distinguished by its less swollen whorls, more elongated aperture with a narrowly reflexed inner margin, and its pale colour. It may be that *L. mweruensis* is only a variant of *L. truncatula* and that this species has a widely scattered distribution in the highlands of North-east Africa, but this can only be established by extensive further collecting.

Lymnaea natalensis (Krauss, 1848)

Limnaeus natalensis Krauss. var. *exsertus* v. Martens, 1866.
Limnaea orophila Morelet, Jickeli, 1874.
Limnaea africana Bourguignat, 1883.
Limnaea caillaudi Bourguignat, 1883.

Limnaea gravieri Bourguignat, 1883.
Limnaea acroxa Bourguignat, 1883.
Limnaea exserta v. Martens, 1897.
Radix pereger (Müller). Piersanti, 1940.

Localities : 2 (8) ; 4 (6) ; 5 (8).

There is considerable variation in the shell shape (Pl. 8), although in all the specimens the spire is moderately well developed and the majority resemble *L. natalensis caillaudi* as illustrated by Mandahl-Barth (1954). A few smaller specimens with more exserted spires resemble Mandahl-Barth's figures of *L. exserta* v. Martens, but the prostate, instead of being of the cylindrical shape that he describes as being typical of *exserta*, is widely dilated distally as in *natalensis* (Text-fig. 31). The genital system is shown in Text-fig. 30 ; a transverse section through the prostate shows a single internal fold (Text-fig. 32). A large number of the lateral radula teeth show a tendency to a reduction of the endocone resulting in a bicuspid condition (Text-fig. 33).

DISCUSSION

The material on which this paper was based was collected from a relatively small area during a period of about six weeks of the rainy season from September to October, 1957. It cannot be claimed, therefore, that it is completely representative of the freshwater gastropod fauna of the Ethiopian highland region, but there is little doubt that the collection contained the majority of the species that occur in the Chokke Hills. Any conclusions which may be drawn from the results of this work must therefore be qualified by this geographical and seasonal restriction, but such conclusions may have wider application and it is to be hoped that this account will provide a basis for further investigations.

In discussing the fauna of any closely defined area it is often as important to account for the absence of species that might reasonably be expected to occur there as it is to consider those species that have been found. Deficiencies are only significant when the collections have been as exhaustive and thorough as they were in the present case. It is probable that the absence of members of the *Bulinus africanus* and *B. forskali* species complexes, also of any prosobranch snails, can be accounted for by climatic conditions mainly due to altitude, for members of these groups occur in similar latitudes at lower levels. Neuville & Anthony (1906) reported *B. africanus* from the Addis Ababa region at an altitude of about 8,000 ft., and Ayad (l.c.) found large numbers of *B. globosus* in both Lake Tana (6,000 ft.) and the River Abbai at a point 2 miles from its source in the Lake. The type locality of *B. abyssinicus* is in Southern Ethiopia and specimens from Somalia have been studied by Mandahl-Barth (1957*c*). There are no reports in the literature of members of the *B. forskali* group anywhere in the higher regions of Ethiopia, but they have been recorded from all of the surrounding territories. It is well known that the freshwater prosobranchs in Africa are restricted to lower altitudes but the absence of the Ancylidae is surprising for it is a widely distributed family and the descriptions of the habitats investigated appear to be quite suitable for the requirements of its members.

Of the six species described in this paper five are truly African but the sixth, *Lymnaea truncatula*, is a ubiquitous palaearctic species. On the evidence at present

available it is impossible to determine whether the Ethiopian populations are relicts of a distribution that was formerly more widespread, or whether they are a recent introduction by man or migratory birds. The occurrences of this species reported from South Africa may not be in any way connected with the Ethiopian foci and are more likely to be a recent human importation. If birds are held responsible for their transport it is surprising that there are not more palaearctic gastropod species present which might also have originated in this manner, but this same argument could equally well be used to discount the idea of relict populations. *Ancylus fluviatilis* Müller is another palaearctic species that is generally believed to occur in northern Ethiopia (Walker, 1914 and Pilsbry & Bequaert, 1927) although no specimens appear to have been collected since those originally described by Blanford and Jickeli. The possibility that *L. mweruensis* may be a local form of *L. truncatula* confined to highland regions further to the south in East Africa cannot be overlooked, for there must be a fairly effective isolation between populations of a species which is confined to highland areas, and such isolation could easily give rise to distinct local forms. There are a number of species of insects that are endemic to particular massifs in Ethiopia (Scott, 1958) and there is every reason to expect the evolution of local races in other groups.

Of the five purely African species present *Bulinus sericinus* presents the most interesting problems. It has been pointed out in the descriptive section of this paper that *B. sericinus* has been considered at various time to have affinities with both *B. truncatus* and *B. tropicus* and that it is now considered to be a subspecies of *B. truncatus* (Mandahl-Barth, 1960). Observations on the morphology of the present material certainly support the idea of a relationship with the *truncatus* group. However, it has been found in the laboratory that the North African and Middle Eastern forms of *truncatus* do not breed easily at temperatures below 25° C., while *sericinus* is able to maintain itself at altitudes at which the maximum temperature does not reach this level, and may fall to freezing point at night. Further, Ayad points out that there is evidence that *B. sericinus* does not act as an intermediate host of *Schistosoma haematobium* in Eritrea which is in contrast to the characteristic host rôle of species of the *truncatus* group.

It is also premature to regard *Biomphalaria rueppelli* as a synonym of *B. pfeifferi*, although they are undoubtedly closely related ; *rueppelli* from the Sudan breeds easily in the laboratory but considerable difficulty has been experienced with the establishment of colonies of *pfeifferi* from several localities. Epidemiological evidence points to *rueppelli* as the intermediate host for *Schistosoma mansoni* in Ethiopia although this parasite is not common in the highland areas.

The three remaining species, *Anisus natalensis*, *Gyraulus costulatus* and *Lymnaea natalensis* have a very wide distribution throughout Africa and their presence in this collection is not remarkable. Their altitude limits appear to be about 9,000 ft. and beyond this level *Lymnaea truncatula* was the only freshwater gastropod collected.

Although *Bulinus sericinus* and *Biomphalaria rueppelli* appear to be abundant in the highlands of Ethiopia and are the potential intermediate hosts of *Schistosoma*, there are relatively few records of *haematobium* or *mansoni* infection and it is probable that the average temperatures are too low for satisfactory development of the larval

flukes within the snails. Schwetz (1951) reported the occurrence of *S. mansoni* in *B. pfeifferi* from Lake Bunyoni at 6,000 ft. in Uganda and claimed that this was apparently the highest altitude record for the transmission of the disease. It is possible that the small number of records of schistosomiasis from highland areas is due to the small scale or absence of medical surveys. If in fact the disease is more widespread than is thought, it may depend on being continually introduced by the movements of human hosts from lower altitudes in areas where conditions are suitable for continuous local transmission. Until contrary facts are available it must be assumed that suitable conditions exist in Ethiopia for a great extension of schistosomiasis infection with the impending development of the country and increased population movements.

SUMMARY

1. The internal and external morphology of six species of freshwater gastropod molluscs collected in the vicitinity of Debra Markos (8,100 ft.) by the Cambridge Botanical Expedition to Ethiopia 1957 is described. The species are: *Bulinus sericinus* (Jickeli), *Biomphalaria rueppelli* (Dunker), *Gyraulus costulatus* (Krauss), *Anisus natalensis* (Krauss), *Lymnaea truncatula* (Müller), and *Lymnaea natalensis* Krauss.

2. Evidence is presented to show that *Bulinus shackoi* (Jickeli) represents an extreme form in a continuous range of variation within *Bulinus sericinus* (Jickeli). *B. sericinus* is regarded as being closely related to *B. truncatus* (Audouin), but reasons are given for preserving its distinct status within the *truncatus* group.

3. A small species of planorbid which closely resembles *Anisus abyssinicus* (Jickeli) conchologically has been assigned to *A. natalensis* (Krauss) after study of the internal anatomy of the Ethiopian and South African material. The structure of the penis differs from all previous descriptions of species of *Anisus* and related genera.

4. Differences have been found between the large samples of *Lymnaea truncatula* collected and the type specimen of *L. mweruensis* Connolly, the significance of which can only be assessed when further material from the type locality of the latter species is available.

5. The absence from the collection of species that are widespread in freshwaters over the rest of Africa is discussed.

APPENDIX

Climate

Although there is some rainfall in every month of the year in the Ethiopian Highlands, two distinct wet seasons occur, the " little " rains in the early part of the year and the main rains that last from the beginning of July to September in the vicinity of Debra Markos.

The expedition made daily recordings of rainfall, and maximum and minimum temperatures, and comparable data were obtained from Debra Markos airfield. Midday temperatures at Camp 1 (9,800 ft.) were about 15° C. and the average night minimum 7° C. At Camp 2 (11,700 ft.) the extremes were more marked, at midday the temperature often rose above 21° C. and at night fell to freezing point.

Geographical Positions of Collecting Points

Camp 1. Eight miles south-west of Mt. Talo and 20 miles north of Debra Markos, on the " old Italian road " running across the mountains to Mota. Close to a Wednesday hill-top market. 37° 48′ E., 10° 31′ N. 9,800 ft.

Camp 2. About 28 miles NNE. of Debra Markos. On the ridge known as Arat Makereke just below the easternmost and largest of the peaks, above the village of Arogay Amba. 37° 48′ E., 10° 35′ N. 11,700 ft.

Collecting Stations

1. Ussata Stream near Nug-Oil plant, Debra Markos. 37° 43′ E., 10° 30′ N. 8,100 ft. Stream flowing rapidly through marshy meadowland. Exposed to the sun, with brown muddy water and a few still bays at the edges. *Callitriche* and *Polygonum* present. Dry from February to April inclusive.

2. Abbain stream, 2 miles south of Debra Markos by Addis Ababa road. 8,000 ft. Slow flowing, with muddy water and rushes at the edges. Average width 12 ft., maximum depth 6 ft.

3. Small stream arising from a spring near Abbain stream, 37° 45′ E., 10° 03′ N. 7,800 ft.

4. Stream 4 miles west of 37° 45′ E., 10° 03′ N. 7,800 ft. Slow flowing with muddy water and bottom. 10–20 ft. wide, more than half filled with tall rushes. Dammed to make a bathing pool.

5. Large stream by ford at Ejubi, 15 miles south of Debra Markos. 7,900 ft. Very slow flowing and muddy with wide marshes. Choked with rushes except at ford.

6. Small stream, 1–10 ft. wide, with marshy depressions, 20 miles north of Debra Markos. 37° 48′ E., 10° 31′ N. 9,9000 ft.

7. Temporary marsh with vegetation of wet meadow type with *Ranunculus* and *Carex* dominant, 9 miles north of Debra Markos. 8,600 ft.

8. Similar to 7. 10,000 ft.

9. Marshy seepage area ½ mile from Camp. 2. 12,000 ft.

10. Small fast flowing clear stream, 28 miles NNE. of Debra Markos. 37° 48′ E., 10° 35′ N. 11,700 ft.

11. Temporary marsh beside Ussata stream in Debra Markos (locality 1).

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List of Labels used in Figures

ag—albumen gland
an—anus
ca—carrefour
cvd—cut end of vas deferens
ic—interstitial cusp
imr—intermediate mantle ridge
k—kidney
lpl—left pilaster
lpp—lumen of preputium
mc—mantle collar
mct—cut edge of mantle
med—median rectal ridge
n—cell nucleus
ng—nidamental gland
ot—ovotestis
ov—oviduct
p—penis
pa—papilla
pb—pseudobranch
pc—pericardium
pd—distal part of prostate
pf—prostate fold
pp—preputium
pr—prostate
ps—penis sheath
rm—retractor muscles of preputium
rr—lateral rectal ridge
rpl—right pilaster
s—transverse septum
sp—spermatheca
spd—spermathecal duct
ur—ureter
ut—uterus
vd—vas deferens
vs—vesicula seminalis

PLATE 8

Top row : left—*Lymnaea natalensis* (Krauss), form resembling *L. exserta* (Martens), from locality 1 (×3) ; right—*L. natalensis*, form resembling *L. natalensis caillaudi* (Bourguignat), from locality 1 (×3).

Middle row : left—*Lymnaea truncatula* (Müller), locality 6 (×6) ; right—*L. mweruensis* Connolly. Type specimen from Mweru, Mt. Kenya (×6).

Bottom row : *Bulinus sericinus* (Jickeli), left to right—typical form from locality 1 (×4) ; "*shackoi*" form from locality 1 (×4) ; ribbed form from locality 3 (×4) ; inflated form from locality 2 (×4).

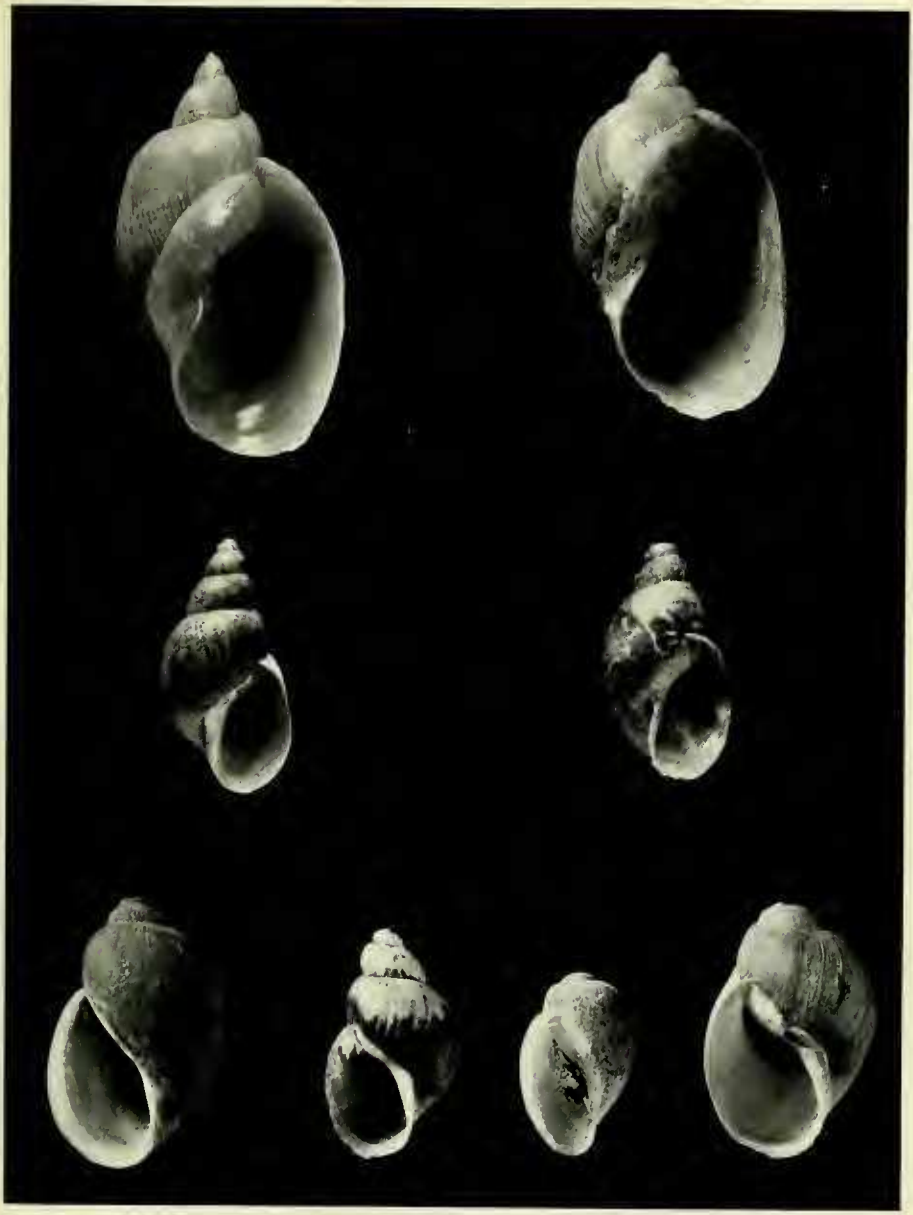

PLATE 9

Top row : *Biomphalaria ruepelli* (Dunker), from locality 3 (×3) (Apertural view ×4).
Second row : *B. rueppelli*, " *adowensis* " form from locality 3 (×4).
Third row : *Anisus natalensis* (Krauss) from locality 4 (×6).
Fourth row : *Gyraulus costulatus* (Krauss) from locality 3 (×6).